THEORETICAL EXPLANATIONS OF THE DISTRIBUTION OF SOUTHERN FAUNAS.

By Captain F. W. Hutton, F.R.S., Hon. Memb. L.S.N.S.W.

On considering the present geographical distribution of land and purely fresh-water vertebrates the first and most obvious generalisation is that while the same or closely allied species are widely spread in the northern hemisphere—through Europe, Asia, and N. America—there is, in the southern hemisphere, a great difference between those inhabiting S. Africa, Australasia, and S. America. When we turn our attention to the marine vertebrates—including the migratory fishes which pass a part of the year in fresh water—we notice that the opposite is the case; for while closely related species are widely diffused in the southern hemisphere, the seals, whales, sea-birds and fishes of the N. Pacific differ considerably from those of the N. Atlantic. The reason for these peculiarities is, of course, the peculiar configuration of the land and sea, giving most of the land to the northern and most of the sea to the southern hemisphere; and a necessary conclusion is that the present configuration of the oceans and continents must have remained much as it is now for a very long time. Indeed oceans and continents could not have been widely different from what they now are ever since most of the present genera—and in some cases even families—of birds and mammals came into existence; for, if such had not been the case, we should not now find these genera and families isolated from each other by barriers of land in the northern, and of sea in the southern hemisphere. We may, therefore, safely infer that the physical geography of the earth has not altered greatly during the latter half of the Tertiary era.

But when we pass from the general aspect of the question to study the details, we find many exceptions (especially in the distribution of the land plants and land animals of the southern

hemisphere) which do not bear out the conclusion forced upon us by the majority of the facts, and the question arises : Have these relationships been brought about by the former existence of more land in the southern hemisphere, or can they be explained without any such assumption ?

The first discussion of the question was by Sir Joseph Hooker, who, in 1853,* advocated a "larger and more continuous tract of land than now exists" in the Antarctic Ocean to explain the distribution of the flowering-plants of the Southern Islands. He assigned no date to this extension of land, but, no doubt, supposed it to be not very ancient.

In 1870, Professor Huxley, in his Anniversary Address to the Geological Society of London, said that the simplest and most rational mode of accounting for the differences between the mammalian faunas of Australia, S. America, and Arctogæa, as well as for the sudden appearance of Eutheria in the latter and in S. America, is the supposition that a Pacific continent existed in the Mesozoic era which gradually subsided, Australia being separated at the end of the Triassic period before the higher mammalia had come into existence. These Eutheria subsequently migrated into North and South America when the Pacific continent finally sank. He says :—"The Mesozoic continent must, I conceive, have lain to the east, about the shores of the N. Pacific and Indian Oceans, and I am inclined to believe that it continued along the eastern side of the Pacific area to what is now the province of Austro-Columbia, the characteristic fauna of which is probably a remnant of the population of the latter part of this period."†

In 1873 I proposed the following hypothesis to explain the complicated problem of the origin of the New Zealand fauna. An Antarctic Mesozoic continent which subsided in the upper Cretaceous period. During the Lower Eocene a second extension of land from New Zealand northwards so as to include New

---

* Flora Novæ Zealandiæ, Introduction, p. xxi.

† Quart. Journ. Geol. Soc. Vol. xxvi. p. lxiii.

Caledonia and part of Polynesia. Subsidence in the Oligocene and Miocene, followed by a third elevation in the Older Pliocene when New Zealand was connected with the Chatham Is., Auckland Is., and perhaps others to the south, but did not stretch north into Polynesia. This large island was broken up by subsidence during the Newer Pliocene.*

In 1874 Prof. A. Milne-Edwards presented to the Academy of Sciences, Paris, a report on the fossil birds of the Mascarene Islands showing that they were related to those of New Zealand. As an explanation, he supposed that land communication had formerly existed between these islands and New Zealand, which was also joined to some islands in Polynesia, while it remained separated from Australia. The connection with Polynesia was to explain the occurrence of *Rhinochetus* in New Caledonia and *Didunculus* in Samoa.

In 1876 Prof. H. N. Moseley supported Sir Jos. Hooker's theory of a former greater extension of land in the Antarctic Ocean†; and in the same year Mr. A. R. Wallace published his "Geographical Distribution of Animals," which treats of the whole question.

In 1880 Mr. Wallace published "Island Life," in which he proposes the following hypothesis relating to Australia and New Zealand. During the Cretaceous period, and probably throughout a considerable portion of the Tertiary era, S. W. Australia (including the southern part of S. Australia) was separated from Eastern Australia by a broad sea, which contained some islands in what is now Northern Australia. This western island had received its mammalia at an earlier epoch from Asia, and no mammals existed in Eastern Australia. New Zealand was connected with the northern part of Eastern Australia, the land forming a horse-shoe open towards the Tasman Sea. Probably the Bampton Shoal, west of New Caledonia, and Lord Howe's Island formed the western limits of this land; but it is possible, though hardly probable, that

* Trans. N.Z. Inst. Vol. v. p. 227, and A.M.N.H. Ser. 4, Vol. xv. p. 25.

† Linn Soc. Journ. Botany, Vol. xv. p. 485.

it extended northward to the Kermadecs and even to Tonga and Fiji. Whether it also extended to the Chatham Islands and Macquarie Island we have, he says, no means of ascertaining, but such is possible. Separation of New Zealand from Australia took place at the close of the Cretaceous period, or in the early Tertiary. At a somewhat later date a southern extension of New Zealand towards the Antarctic continent seems probable "as affording an easy passage for the numerous species of South American and Antarctic plants, and also for the identical and closely allied fresh-water fishes of these countries."*

In 1882 M. Emile Blanchard contributed a paper to the Academy of Sciences, Paris, called "Proofs of the subsidence of a Southern Continent during recent Geological Epochs."†

In 1884-5 I made a further contribution to the subject,‡ in which I abandoned my former idea of a Mesozoic Antarctic Continent, and substituted for it a Mesozoic Pacific Continent, stretching, more or less completely, from Melanesia to Chili. I still adhered to the other portions of my former paper, but laid more stress than before on a greater extension of Antarctic islands during the Older Pliocene.

In 1888 Dr. Theodore Gill published, in the Memoirs of the National Academy of Sciences, Philadelphia, a paper called "A comparison of Antipodal Faunas," in which he also advocated the existence of "some terrestrial passage way" between Tasmania, New Zealand, and South America, "at a time as late as the close of the Mesozoic period. The evidence of such a connection afforded by congeneric fishes is fortified by analogous representatives among insects, molluscs, and even amphibians. The

---

* Island Life, p. 455.

† See N. Z. Journal of Science, Vol. i., p. 251. In the same Journal will be found a paper by Dr. H. Filhol on the Geological and Zoological Relations of Campbell Island with the neighbouring Islands.

‡ Part I. in N. Z. Journ. Sci. Vol. ii. p. 1, and A. M. N. H. (5), xiii., 425; Part II. in N. Z. Journ. Sci. Vol. ii. p. 249, and A. M. N. H. (5), xv., 77.

separation of the several areas must, however, have occurred little later than the early Tertiary, inasmuch as the salt-water fishes of corresponding isotherms found along the coasts of the now widely separated lands, are to such a large extent specifically different."

In 1892 Dr. H. von Jhering published a paper in the Trans. N. Z. Inst. Vol. xxiv. "On the Ancient Relations between New Zealand and South America." He here supposes that during the whole of the Mesozoic era a continent—which he calls Archiplata —existed which included Chili and Patagonia and extended into the South Pacific. This gradually subsided, throwing off first the Polynesian Islands, then New Zealand, and finally New Guinea and Australia. All this took place before and during the Eocene period; after which Archiplata was joined to Archiguyana, which occupied the high lands of Brazil and Venezuela. Dr. F. Ameghino has also, quite independently, advocated a Pacific Mesozoic continent to explain the relations of the Eocene marsupials of Patagonia to those of Australia, and Prof. Zittel has expressed a favourable opinion of this theory.*

In 1893 Dr. H. O. Forbes published a paper in the "Geographical Journal (Supplementary Papers") called "The Chatham Islands: their relation to a former southern continent," in which he reproduced the old theory of an Antarctic continent, but made it last until late Pliocene times, when, he thinks, the Antarctic fauna and flora were driven north by the coming on of a glacial epoch. This continent is supposed to have been unconnected either with S. Africa or with W. Australia (which formed a large island); but sent out prolongations northward, (1) to Madagascar and the Mascarene Islands, (2) to Tasmania and E. Australia, thence through New Guinea and the Solomon Islands to Borneo and Sumatra, (3) to New Zealand, New Caledonia and Fiji; and (4) to S. America, reaching to beyond the Amazon.

In the same year Mr. C. Hedley published in the Proc. Linn. Soc. N.S.W. a short note advocating the existence during Mesozoic

* See Geol. Mag. New Series, Decade iii., Vol. 10, p. 512 (1893).

and early Tertiary times of a strip of land extending from S. America across the pole to Tasmania; New Zealand, in Tertiary times, reaching near this antarctic land without joining it. And in "Natural Science" he had a paper "On the Relations of the Fauna and Flora of Australia to those of New Zealand," in which he supports the idea of an ancient continent, or "Melanesian Plateau,"* which included the Solomon Islands, Fiji, New Hebrides, New Caledonia, Lord Howe Island and New Zealand, but was separated from Australia and New Guinea. No date is given to this island-continent, but it is supposed to be later than the "Australian Tertiary and Mesozoic beds"; later, therefore, than the Antarctic land.

In 1895, Mr. Hedley returned to the subject in a paper to the Royal Society of N.S.W. called "Considerations on the surviving Refugees in Austral Lands of ancient Antarctic Life." Here he advocates an Antarctic continent, which was a very unstable area, "at one time dissolving into an archipelago, at another resolving itself into a continent." He thinks that snakes, frogs, monotremes and marsupials passed across this continent, from S. America to Tasmania, during a warm, Mid-tertiary period. He also now thinks that the southward extension of New Zealand, mentioned in his former paper, was synchronous with its northern extension to the Melanesian plateau; that is, it was late instead of early Tertiary date.

This short historical sketch will, I think, make it clear that a considerable amount of ingenuity has been expended in trying to solve the interesting problem of the distribution of southern faunas. The differences of opinion are due partly to some of the authors having taken only a small number of the known facts into consideration, and partly to constant additions to our knowledge; either by the discovery of new facts, or by the correction of old errors. No doubt our knowledge will still increase, but it seems hardly possible to make any more theories. The problem is a very intricate one, and we may be sure that the true solution is not simple.

---

* Called Antipodea by Dr. Forbes.

It is evident that in any large district, like Australasia, there is no reason to suppose that the ancestors of the animals and plants now inhabiting it all came from the same direction or at the same time : consequently the first step to take is to try to separate the fauna and flora into groups which find their nearest relations in different directions. Thus in Australasia we have—

1. An Australasian fauna and flora which have no near relatives now living.

2. A northern fauna and flora related to the Oriental fauna and flora of the present day.

3. A south-tropical or sub-tropical fauna and flora whose nearest relations at present are either in S. Africa or in S. America north of 40° S. That the differences between these countries are far greater than their resemblances does not do away with the existence of these resemblances, but rather accentuates them. They are vestigial remains with all the importance that vestigial remains always possess.

4. A south-temperate or cold-temperate fauna and flora, with relations to plants and animals in Patagonia or Chili and the Antarctic Islands. This is usually called the Antarctic element.

Judging by the relative closeness of the relationship of these different faunistic elements to their foreign connections, we must conclude that the first and third are much older inhabitants of Australasia than the second and fourth. The second element, which is best developed in north-eastern Australia, presents no difficulty and everyone is agreed as to its origin. The fourth element, which is better developed in New Zealand than in any other part of Australasia, consists of marine animals with a few migratory fresh-water fishes and possibly some land mollusca and worms; and there is a general consensus of opinion that these spread by means of a greater development of land in the Antarctic region. This may have been as late as the Older Pliocene, but not later, as considerable changes have taken place in the animals since it occurred. Also, as pointed out in the first paragraphs of this paper, this land could not have been continuous between S.

America and Australasia, for in that case there would have been a far greater commingling of the land faunas and floras. It is the origin of the first and third elements which has given rise to such differences of opinion. These are developed far more strongly in Australia and Tasmania than in New Zealand; and the explanation of the third will probably explain the first also. I will, therefore, briefly review the three hypotheses (variously modified) which have been proposed.

1. The first explanation is that the different groups of animals and plants in question have migrated from the northern hemisphere into the southern by the present continents and have since then become extinct in the north. With regard to the South African connection, this explanation will be readily accepted. The fact that Proteaceous plants—now almost confined to S. Africa and Australia—were formerly abundant in Arctogæa is a proof, so far as they are concerned; and we may accept the same explanation for the occurrence of the Baobab-tree *(Adansonia)* in W. Australia and the Fern-bird *(Sphenœacus)* in New Zealand. This theory also explains the occurrence of the curious genus of wingless locusts—*Anostostoma*—in Madagascar and Australia and the connection of some birds of Madagascar and the Mascarene Islands with others of New Zealand and Polynesia. It will also explain the abundance of parrots in Australia and S. America, for these lived in Europe in the Miocene period, as well as the occurrence of tapirs and trogons in Central America and Malaya; for these, like the large carnivora, must have passed from one continent to the other by a northerly passage. Probably also it will explain the relation of the curassows of S. America to the megapodes of Australia and Polynesia, and the connection between the lower passerine birds of both continents, as these relationships are all very distant.

But, however this may be, there are certain facts of distribution which this theory cannot solve. A typical case is the distribution of the tree-frogs belonging to the genus *Hyla*. This contains 83 species in S. America, 28 in Australia, 17 in N. America, and one each in India, China, and Europe; while *Hylella* is found

only in Australia and tropical America. Again the fresh-water tortoises belonging to the family *Chelydidæ* are restricted to Australia and S. America. The fresh water fish *Osteoglossum* is represented by species in S. America, Queensland, and Borneo; and the South American beetles are more closely related to those of Australia and Africa than they are to those of N. America. Indeed the connection between S. America and Australia is so marked in the *Buprestidæ* and *Longicornia* that Mr. Wallace, who as a general rule strongly supports the northern route, says that "there must probably once have been some means of communication between the two regions better adapted to these insects than any they now possess." And as several of the Eocene mammalia of Patagonia were closely allied to those now living in Australia the evidence for a former land passage between the two countries may be considered as conclusive. The northern route therefore fails to give a full and satisfactory account of the whole of the facts, and we must look to some other route to supplement it. The portions of the faunas unaccounted for are all old forms of life, and consequently we must conclude that the means of communication used by them has been long ago destroyed; for if not it would also have been used for modern groups.

2. Turning now to the proposed southern route by an Antarctic continent, it has this in its favour that, as the greater extension of Antarctic land in the late Tertiary era has been allowed, it is not difficult to suppose that at a still earlier time, that is in the Mesozoic era, a large continent might have existed there. One difficulty is in the climate. How could tropical, or sub-tropical, snakes, insects, and fresh-water tortoises and fishes pass through such high latitudes? The example of Greenland is pointed to, but in Greenland the climate indicated is temperate only, not sub-tropical or tropical. Again it is stated, in explanation, that there is evidence of a much warmer climate having obtained in the southern hemisphere in Miocene times than now. But this appears to have been a period of depression throughout southern Australasia, and it does not follow that the climate would be equally mild when an Antarctic continent existed. I do not

think that the climatic objection is fatal, for we cannot tell what the climate may have been in the Jurassic and Cretaceous periods, but it is a difficulty, and I cannot go so far as Mr. Hedley, who supposes that venomous snakes, frogs, monotremes and marsupials passed round the head of a deep bight of the Pacific Ocean which "stretched within a few degrees of the pole."

A far greater difficulty remains for consideration, which is this: Aplacental Mammals — both Multituberculata and Polyprotodontia—existed in Europe and N. America in the Triassic and Jurassic periods, and these Polyprotodontia were, no doubt, the ancestors of the living Polyprotodontia of Australia. In the Eocene strata of Patagonia remains of a large number of Polyprotodontia have been found which are far more closely related to the Polyprotodontia of Australia than to the Mesosoic forms of Europe and N. America; consequently a direct land communication must have existed between these two southern countries. Now there is strong geological and palæontological evidence that no land ridge existed between N. and S. America during the Mesozoic and early Cainozoic eras; consequently we must assume that the southern forms migrated through the Malay Archipelago; and, if they went to Patagonia by means of an Antarctic continent, they must have passed through Australia. But mingled with the Eocene marsupials of Patagonia there are a number of Eutheria of typically South American character—*Edentata*, *Toxodontia*, *Typotheria*, *Perissodactyla*, *Rodentia*, and even *Platyrrhine* monkeys—without any northern forms of *Artiodactyla*, *Carnivora*, or *Insectivora;* and it is hardly possible that these should have passed through Australia without leaving any record behind. This is, to me, a fatal objection to the theory of migration by means of an Antarctic continent.

3. The theory of the former existence of a South Pacific Mesozoic continent seems to be the only theory left; but it has been objected to both on account of the present depth of the ocean and because, it is said, no record has been left in the Polynesian Islands of the supposed passage of the plants and animals. Both these objections apply equally to the former

existence of an Antarctic continent. According to the latest maps the ocean south of Tasmania, and the Pacific below 45° S., are considerably deeper than the Pacific between 10° and 30° S., and the answer in both cases is that this continent existed a very long time ago. The answer to the second objection is that no record has been preserved of the fauna and flora on the Antarctic continent because of a change in climate, and in the Polynesian Islands because the continent disappeared entirely below the sea, the present volcanic and coral islands being merely outgrowths on its submerged back. But the statement that no record exists in the case of the Pacific continent is not quite correct, for the Iguanas of Fiji can hardly be explained in any other way.

The theory of a Mesozoic South Pacific continent not only explains the origin of the Australian and S. American marsupials, but also the almost simultaneous appearance of different Eutherian mammals in North and South America. We must suppose that this continent threw off first New Zealand, then Australia, then Chili, and finally disappeared under the waves. The reasons why we must suppose New Zealand to have been at one time attached to the continent are the existence in that country of *Sphenodon*, *Unio*, and *Astacidæ*, none of which are found in truly Oceanic islands*. At a later date, as I pointed out in my former papers, New Zealand must have formed part of a large island joined to New Caledonia, but not to Australia. This has lately been called Antipodea by Dr. Forbes, and the Melanesian Plateau by Mr. C. Hedley. Still later again, New Zealand must have stretched south and obtained its Antarctic fauna and flora from Patagonia through a number of islands.

From a biological point of view I see no reason to object to this theory. The objections are geological, and most geologists at the present day would, I think, say that the doctrine of the persistence

* It is also hardly possible to account for the distribution of frogs, slugs, wingless and feebly flying insects, earth-worms, myriapods, and fresh water animals generally, except by the supposition of land passage.

of continental and oceanic areas negatives it. This doctrine—which is not accepted by all geologists*—is founded on the undoubted fact that the principal mountain ranges in the northern hemisphere, and, perhaps, in Australia also, are formed of shallow water sediments representing all periods from the Silurian upwards; consequently land must have existed in their neighbourhood all that time; and from this it is inferred that the present oceanic areas have always been sea. The proof, however, is far from being complete, and no explanation has, as yet, been given either (1) of the remarkable submarine plateaux found in the basins of the S. Pacific and S. Atlantic Oceans; or (2) of the sudden irruption of mollusca, bony-fishes and dicotyledons into N. America during the close of the Cretaceous period, followed by a host of Eutherian mammalia in the Eocene; or (3) of the place of origin of the peculiar S. American mammalia. The former existence of a Mesozoic Pacific continent seems to me, as it did to Professor Huxley, the simplest explanation of all these difficulties; we can never expect to attain certainty in the matter, but I think that the weight of the evidence is in its favour.

* Gardner, Geol. Mag. 1882, p. 546; Hutton, N.Z. Journal of Science, Vol. I. p. 406 (1883); Blandford, Q.J.G.S. XLVI. Proceedings, p. 59 (1890); Oldham, Geol. of India, 2nd Ed. p. 211 (1893).